

Growth Rate of Jamaican Coral Reef Sponges After Hurricane Allen*

CLIVE R. WILKINSON AND ANTHONY C. CHESHIRE

Australian Institute of Marine Science, P.M.B. No. 3, Townsville M.C. 4810, Queensland, Australia

Abstract. Growth rate estimates for five coral reef sponges on the Discovery Bay fore-reef are presented. These were determined from the size of individual sponges growing on the coral rubble that was deposited when Hurricane Allen struck the north coast of Jamaica in August 1980. Sponges collected in February 1986 were weighed and their growth rates determined using the MIX program, originally developed to analyze size-frequency data in fish populations. Sponge doubling times were between 232 and 304 days, with evidence that early exponential growth may be slowing down after four years. The fastest growing sponges were those with small populations of symbiotic cyanobacteria, indicating that there may be a selective advantage for those sponges with photosynthetic symbionts.

Introduction

Hurricane Allen passed within 50 km of the north coast of Jamaica on 6 August 1980. Large seas generated by winds in excess of 250 km per hour caused extensive damage to the coral reefs in the vicinity of the Discovery Bay Marine Laboratory (Woodley, 1980; Woodley *et al.*, 1981). The damage, however, was patchy; it was extensive in some areas and minor in those areas where local topography resulted in the attenuation or deflection of the waves (Woodley *et al.*, 1981). Prior to the hurricane, the fore-reef slope contained extensive, dense thickets of *Acropora cervicornis* between 10 m and 25 m (Goreau and Goreau, 1973; Pang, 1973). Some of these thickets were destroyed, resulting in the deposition of coral rubble which buried other sessile invertebrates.

Prior to Hurricane Allen, sponge populations on the fore-reef slope of Discovery Bay were large (Reiswig, 1973) and considered to be ecologically significant as they could filter a volume of water equivalent to the entire water column to a depth of 40 m each day (Reiswig, 1974). The only evidence of these populations in February 1986 was below 30 m depth where some of the extensive populations reported by Reiswig (1973) remained.

Reliable estimates of the growth rates of marine sponges generally are not available. Reiswig (1973), Dayton *et al.* (1974), and Wilkinson (1978) all attempted to determine growth rates by measuring sponges underwater, however their estimates were not particularly successful. More accurate estimates were obtained by Wilkinson and Vacelet (1979) who transplanted Mediterranean species onto plastic plaques for subsequent periodic measurement. These techniques, however, involved trauma to the specimens and were time consuming.

Sponge populations were surveyed on the north coast of Jamaica as part of a larger study (Wilkinson, 1987). The site chosen off the Discovery Bay Marine Laboratory was covered by a dense bed of *Acropora* rubble in excess of half a meter thick, which had accumulated during Hurricane Allen. This bed covered large areas with no evidence of the previous coral or sponge fauna. The site, however, did contain numerous small sponges and coral colonies growing on pieces of the rubble. This study reports the estimated growth rate of one sponge species from 20 m on the fore-reef slope off Discovery Bay. Four other species were collected, and speculative doubling rates are presented based on the rate estimated for the first species, *Pseudoceratina crassa*.

Materials and Methods

Specimens of five massive sponge species were collected in February 1986 from 20 m depth, approximately

Received 26 August 1987; accepted 20 May 1988.

* Contribution No. 410 from the Australian Institute of Marine Science and No. 425 from the Discovery Bay Marine Laboratory, Jamaica.

1 km to the west of the Discovery Bay Marine Laboratory (see Goreau and Goreau, 1973, for site description). Care was taken to select only regular-shaped animals (presumably derived from a single larva) which were attached to rubble and without obvious signs of predation damage. The sponges were weighed after draining for approximately 20 seconds and the volume measured by displacement in water. Estimations of dry weight were made on 5 individuals of each species after drying for 36 h at 80°C.

The size-class structure of the *Pseudoceratina crassa* population was estimated using the MIX program of Macdonald and Pitcher (1979; Macdonald and Green, 1986). MIX is an interactive program used to fit distributions to grouped data by maximum likelihood estimation. The program has been used effectively in the analysis of fisheries size-frequency data where the groups represent successive year classes. For *P. crassa*, it was assumed that there were five size groupings representing the recruitment from five annual spawning events between Hurricane Allen and the date of collection. To test this assumption, all possible combinations of groups from two to ten were tried, but a significant fit was only obtained for five groups. The mean size of sponges in each size-class was determined from the significant fit obtained to the size-frequency data with the MIX program. These mean values for each size-class were analyzed using a least squares regression to provide an exponential growth model ($W_t = ae^{\alpha t}$) from which the relative growth rate α was estimated.

Growth rates for the other four sponge species could not be obtained by the same method due to the limited number of specimens. Growth rate approximations for these species were derived using the growth model from *P. crassa*. It was assumed that the average size at 50 days after spawning was the same for all species. Exponential growth curves were then derived using simultaneous equations starting with a wet weight at 50 days of 2.93 g (as for *P. crassa*) and the weight of the largest individuals at the date of collection. The age of these individuals was defined as the number of days between the first spawning after Hurricane Allen and the date of collection. Dates for spawning of these species were extracted from the few observations of mass release of sperm reported in the literature (Reiswig, 1983; Hoppe, 1988).

Results

The most prevalent sponge in this area, *Pseudoceratina crassa*, has an approximate doubling time of 8.5 months (257 days) with individuals after 5 years weighing, on average, 350 g wet weight (Fig. 1; Table I).

Growth rate estimates for the other four sponges suggest that the doubling times are between 7.6 and 10

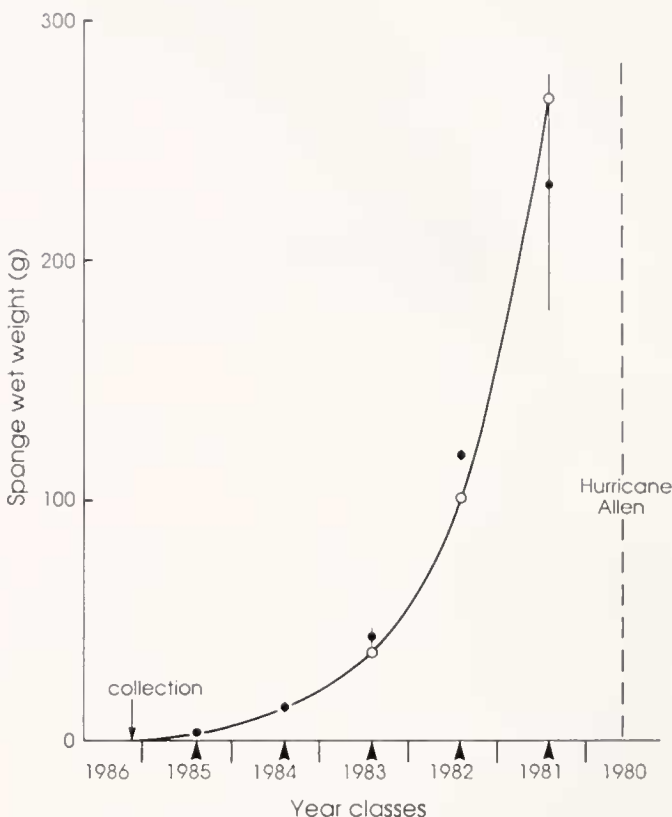


Figure 1. *Pseudoceratina crassa* growth curve prepared from MIX program analysis of sponge wet weights on the collection date in February 1986. The mean size for the five size-classes with standard errors are positioned at the suggested date of spawning (solid arrows) in May of each year. Hurricane Allen occurred on 6 August 1980. The exponential growth curve ($W_t = ae^{\alpha t}$, where $a = 2.567$, $\alpha = 0.00270$, and t = days since spawning) is represented by the curve drawn through the open circles, which are derived "mean sizes" for time year classes.

months (232 and 304 days). These species were less abundant in the area surveyed, hence fewer samples were available for growth rate analysis. Confidence in these estimates is substantially lower than for *P. crassa*, especially for *Agelas dispar* (Table I).

The full data sets for the five species are listed in Figure 2 with the estimated mean size of each year-class. It was assumed that there were five spawning events after Hurricane Allen in August 1980, and that each spawning event contributed individuals to the population. In the case of *Ircinia felix*, the position is different in that there are possibly two annual sperm release events, one in October and another in February. Six year-classes are represented on Figure 2 assuming an October release, although it must be recognized that semi-annual classes could exist. The largest sponges are assumed to have arisen from larvae settling within two months of the hurricane, hence, the estimated growth rates are the most conservative. For the other species, there is a presumed

Table 1

Estimated growth rate parameters for sponge species at 20 m on the fore-reef slope of Discovery Bay, Jamaica

| Sponge | Spawning date used | Abundance m ⁻² | No. collected | Doubling time days | Growth const. α | Growth const. a | Size g 5 years | Dry Wt. | Vol. |
|------------------------------|--------------------------|---------------------------|---------------|--------------------|------------------------|-----------------|----------------|--------------|--------------|
| | | | | | | | | Wet Wt. | Wet Wt. |
| <i>Pseudoceratina crassa</i> | 28 May | 0.57 | 135 | 257 | 0.00270 | 2.567 | 354 | 0.175 ± .021 | 0.946 ± .023 |
| <i>Ircinia felix</i> | 14 February 1 October | 0.12 | 54 | 235 | 0.00295 | 2.535 | 552 | 0.154 ± .032 | n |
| <i>Verongula ardis</i> | 14 March | 0.05 | 39 | 232 | 0.00294 | 2.531 | 587 | 0.108 ± .023 | 0.927 ± .034 |
| <i>Smenospongia aurea</i> | 14 March | 0.02 | 48 | 304 | 0.00228 | 2.621 | 168 | 0.155 ± .013 | .930 ± .050 |
| <i>Agelas dispar</i> | 20 July | 0.05 | 17 | 250 | 0.00277 | 2.557 | 404 | 0.150 ± .013 | n |

Spawning dates used in the exponential equations are from Reiswig (1983) and Hoppe (1988). Abundance reports incidence m⁻² in 120 m² surveys reported in Wilkinson (1987). The doubling times and growth constants α and a are from the exponential equation $W_t = ae^{at}$ which was used to estimate size (wet weight) after 5 years. Dry weight to wet weight and volume to wet weight ratios plus standard deviations are included for comparison with other studies; n, no data available.

lag of 6.3 to 11.5 months between the date of the hurricane and the first spawning event.

Discussion

Hurricane Allen presented the opportunity to estimate the growth rates of some Caribbean reef sponges. These estimates, although approximate, represent rare examples of sponge growth rate statistics at the early stages of growth. A similar opportunity was used by Scoffin and Hendry (1984) to assess the effects of Hurricane Allen on the recruitment of sclerosponges to the Discovery Bay reef.

The estimated growth rates of the five species indicate doubling times in the range 232–304 days, *i.e.*, all increase by more than 100% per annum. These exceed the rates reported during studies of larger specimens of coral reef sponges (Reiswig, 1973; Wilkinson, 1978). These rates are only applicable to young sponges in the early exponential stage of growth, and cannot be extrapolated to larger sponges where proportional growth rates are considerably less (Reiswig, 1973). There is evidence in Figure 1 that the rate of growth of *Pseudoceratina crassa* is slowing down after four years with the fifth year-class sponges being 40 g (15%) smaller than sponges predicted from unrestricted exponential growth. A reduction in growth rates after the early, exponential phases of growth was observed by Reiswig (1973) for three large sponge species on the Discovery Bay reef.

These estimated growth rates are considered more useful than those recorded previously for coral reef sponges. The estimates are conservative as it is assumed that the larger sponges resulted from larvae settling out within the first year of Hurricane Allen. If the larger sponges resulted from later settlements, then more rapid growth rates

would apply. The estimates were based on measurements of differences in biomass (both wet and dry weight measurements), whereas in previous studies growth rates were based on estimated changes in the size of large, irregular specimens underwater.

The assertion that these estimates may be more reliable depends on several assumptions:

- (i) All sponges in the region surveyed were destroyed by the hurricane. The specimens collected originated from newly settled, individual larvae produced by undamaged populations from deeper water;
- (ii) The individuals collected, particularly the large ones, originated from single larvae;
- (iii) The sponge species examined produce recognizable size classes which can be related to annual or semi-annual spawning events;
- (iv) The largest sponges resulted from larvae which settled out within the first year after Hurricane Allen.

With respect to assumption (i), destruction in the region surveyed in 1986 was extensive; no large corals (*e.g.*, *Montastrea annularis*) or sponges survived. The area is seaward of site B in Woodley *et al.* (1981) where there was extensive damage to gorgonian colonies. This site (similar in profile to E in Fig. 1 of Woodley *et al.*, 1981) was fully exposed to wave action because it slopes gently, thereby acting as the final repository for considerable amounts of *Acropora* rubble from shallower depths. Hence, it is unlikely that any sponge fragments survived in this habitat. All sponges appeared to be individuals that had settled on the rubble.

Of the five sponges present in sufficient numbers to warrant collection for this study, three form distinct,

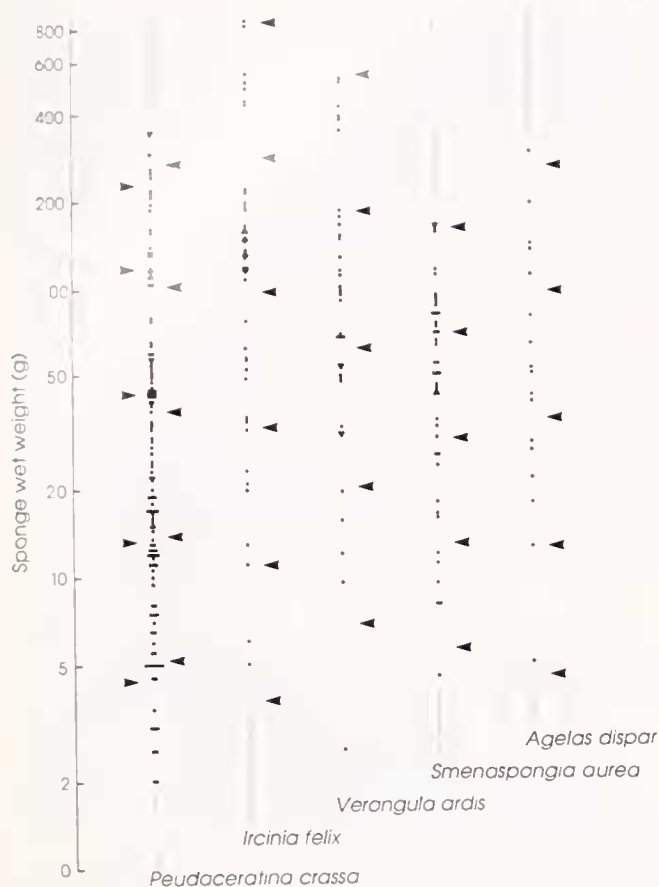


Figure 2. The data set of wet weights (natural logarithmic scale) of the five sponge species from 20 m depth on the Discovery Bay fore-reef. The arrows to the left of the *Pseudoceratina crassa* data set represent the sizes of the year-classes obtained from the MIX program, whereas the arrows to the right of each data set are the year-class sizes from exponential growth curves based on the curve derived from the *P. crassa* data.

massive shapes that vary little with size. *Smenospongia aurea*, *Verongula ardis*, and *Agelas dispar* all are erect, discrete sponges; the first two have a single osculum. It is assumed with confidence that the individual sponges of these three species grew from single larvae. This assumption is more difficult with the other two species. *Ircinia felix* forms irregular, hemispherical mounds which can fuse with adjacent specimens. *Pseudoceratina crassa* commences as a conical-shaped mound with a single oscule. These mounds divide as the sponge grows, eventually forming a series of similar-shaped mounds. Thus, in larger specimens it is difficult to differentiate between larger single sponges and smaller ones that have fused. In all of these sponges, however, it is unlikely that genetically compatible individuals have settled close enough to fuse when individual density is less than 1 m^{-2} . Therefore, the possibility that the larger specimens have

formed from the fusion of smaller individuals is regarded as remote.

Knowledge on sponge age-classes [assumption (iii)] is lacking. Very little is known about sponge reproduction *in situ*, and even less is known of settlement from pelagic larvae. Most reports of periodicity in sponge breeding have come via divers' observations of mass releases of spermatozoa. In general, Caribbean sponges appear to have one or possibly two major spawning events *per annum* (Reiswig, 1983; Hoppe, 1988). For *P. crassa*, there is one report of several individuals spawning in May; another species of *Ircinia* produces mature sperm in September/October and again in February; other verongids like *S. aurea* and *V. ardis* spawn in February/March; and five of six reports for *Agelas* species report a single spawning event in July. From these meager observations, the only conclusion is that there is apparently only one and possibly two spawning events *per annum* for most Caribbean sponges.

After considering these assumptions and the associated constraints, these growth estimates can only be considered indications of the rates for these species until more accurate measures are obtained. If assumption (iv) is incorrect, then these rates underestimate *in situ* growth of these sponges. While the rates apply to only five species at one depth on the Discovery Bay fore-reef, they are indicative of three different Orders. These estimates exceed those reported previously for marine sponges. Reiswig (1973) reported that two species on the same reef had barely detectable growth rates, whereas another species, *Mycale laxissima*, had an annual growth rate of 60%. Wilkinson (1978) reported little or no growth for three species of Great Barrier Reef sponge, but *Neofibularia irata* had a mean growth rate of 33%. The doubling rates reported by Wilkinson and Vacelet (1979) varied from 19 weeks to 1 year, but these were for small Mediterranean sponges measured for the period of optimal growth.

The range of growth doubling times of 7.6 to 10 months at 20 m depth indicates that it will take a minimum of 4 to 6 more years for the sponge biomass to approach that reported to exist prior to the hurricane (Reiswig, 1973) or found on other Caribbean reefs at the same depth where individuals of all 5 species attain sizes in excess of 1 kg wet weight (Wilkinson, 1987). The species composition of the developing sponge population at Discovery Bay is considerably different to that studied by Reiswig (1973). In 1973, there were at least 100 sponge species on the fore-reef slope in front of Discovery Bay, whereas only 20 species were evident in an area of 120 m^2 in early 1986 (approximately half that found on other comparable Caribbean reefs; Wilkinson, 1987).

These apparently rapid rates of sponge growth indicate that there is an adequate supply of organic nutrient.

These species would rely almost entirely on the removal of organic matter from seawater for nutrition as none are phototrophic (Wilkinson, 1983). However, two of the species do have small populations of symbiotic cyanobacteria which may augment the amount of nutrient removed from the seawater through the translocation of fixed nutrient carbon (Wilkinson, 1979). These two sponges, *Ircinia felix* and *Verongula ardis*, showed the most rapid growth rates and it is possible that the increased growth over the other species may be attributable to supplemental nutrition from the symbionts.

Acknowledgments

This research was supported under the U. S./Australia Bilateral Agreement for Scientific and Technological Cooperation and by the Australian Institute of Marine Science. Special thanks are due to Dr. J. Woodley and staff at the Discovery Bay Marine Laboratory and to Madeleine Nowak. Dr. H. Reiswig provided valuable criticism of the manuscript.

Literature Cited

- Dayton, P. K., G. A. Robilliard, and R. T. Paine. 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecol. Monogr.* **44**: 105-128.
- Goreau, T. F., and N. I. Goreau. 1973. The ecology of Jamaican coral reefs. II. Geomorphology, zonation, and sedimentary phases. *Bull. Mar. Sci.* **23**: 399-464.
- Hoppe, W. F. 1988. Reproductive patterns in three species of large coral reef sponges. *Coral Reefs* (in press).
- Macdonald, P. D. M., and T. J. Pitcher. 1979. Age-groups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures. *J. Fish. Res. Board Can.* **36**: 987-1001.
- Macdonald, P. D. M., and P. E. J. Green. 1985. *User's Guide to Program MIX: an Interactive Program for Fitting Mixtures of Distributions*. Ichthus Data Systems, Ontario, Canada. 28 pp.
- Pang, R. K. 1973. The ecology of some Jamaican excavating sponges. *Bull. Mar. Sci.* **23**: 227-243.
- Reiswig, H. M. 1973. Population dynamics of three Jamaican Demospongiae. *Bull. Mar. Sci.* **23**: 191-226.
- Reiswig, H. M. 1974. Water transport, respiration and energetics of three tropical marine sponges. *J. Exp. Mar. Biol. Ecol.* **14**: 231-249.
- Reiswig, H. M. 1983. 1. Porifera. Pp. 1-21 in *Spermatogenesis and Sperm Function*, K. G. and R. G. Adiyodi, eds. John Wiley & Sons, New York.
- Scoffin, T. P., and M. D. Hendry. 1984. Shallow-water sclerosponges on Jamaican reefs and a criterion for recognition of hurricane deposits. *Nature* **307**: 728-729.
- Wilkinson, C. R. 1978. Microbial associations in sponges. I. Ecology, physiology and microbial populations of coral reef sponges. *Mar. Biol.* **49**: 161-167.
- Wilkinson, C. R. 1979. Nutrient translocation from symbiotic cyanobacteria to coral reef sponges. Pp. 373-380 in *Biologie des Spongiaires*, C. Levi and N. Boury-Esnault, eds. Coll. Int. C.N.R.S., Paris, No. 291.
- Wilkinson, C. R. 1983. Net primary productivity in coral reef sponges. *Science* **219**: 410-412.
- Wilkinson, C. R. 1987. Interocean differences in size and nutrition of coral reef sponge populations. *Science* **236**: 1654-1657.
- Wilkinson, C. R., and J. Vacelet. 1979. Transplantation of marine sponges to different conditions of light and current. *J. Exp. Mar. Biol. Ecol.* **37**: 91-104.
- Woodley, J. D. 1980. Hurricane Allen destroys Jamaican coral reefs. *Nature* **287**: 387.
- Woodley, J. D. et al. 1981. Hurricane Allen's impact on Jamaican coral reefs. *Science* **214**: 749-755.